VOLUME XXV NUMBER 5

BOTANICAL GAZETTE

MAY 1898

THE ORIENTATION OF THE PLANT EGG AND ITS ECOLOGICAL SIGNIFICANCE.

CONWAY MACMILLAN.

As a convenient series of forms in which the embryogeny has been carefully investigated one may select the Archegoniatæ. A number of groups in which genuine eggs are developed thus fall outside the limits of discussion. Among these are the Chlorophyceæ with such genera as Sphæroplea and Coleochæte; the Phæophyceæ, particularly Fucus and its allies; and the Phycomycetes, as for example Peronospora and Achlya. The metaspermic types of segmentation will be found to be derived from certain archegoniate types and will receive incidental attention, but it will be quite unnecessary to enter into an examination of the modified and often degenerate processes that succeed the physiological equivalent of fecundation in Rhodophyceæ. With such limitations there will be presented a review, in succinct form, of certain important types of egg segmentation known to occur among the plants classified by Engler as *Embryophyta zoidiogama.*

BRYOPHYTIC ORIENTATION AND SEGMENTATION TYPES.

Among bryophytes the egg manifests in the Hepaticæ all the types of segmentation that are retained in the higher order. Therefore it will be unnecessary to give any special account for the Musci. Essentially all Musci present segmentations that are ecologically equivalent, with the possible exception of Archidium which seems to be a degenerate type rather than rudimentary. The basal type among Musci seems to be that of Sphagnum, which connects closely with the type of Anthoceros among Hepaticæ. In mosses the most important improvement over Hepaticæ, in the embryogeny, is the early differentiation of at least the distal cell of the embryo as an apical cell, while in some cases the proximal cell also accepts this character and organizes the foot by apical segmentations. In Hepaticæ the distal apical cell is the only apical cell developed, and this does not undergo improvement beyond the hemispherical type, so that apical growth in the hepatic embryo is limited.

Embryogeny of Riccia.— Early researches upon the embryogeny of *Riccia glauca* were conducted by Hofmeister,[1] whose account, however, was quite imperfect. His figure (*l. c. pl. 10, fig. 9*) shows a rather abnormally inclined basal wall. Our exact knowledge of the early stages in this embryogeny are due to Kienitz-Gerloff,[2] who corrected the errors in the original account of Hofmeister and figured the early stages (*l. c. pl. 3*) from the primitive segmentation to the specialization of amphithecium and endothecium. Leitgeb[3] considered the embryogeny of this plant and shows (*l. c. pl. 2, fig. 8*) an early stage in the embryogeny with the normal slightly inclined basal wall. The accompanying figure (*fig. 1*) represents diagrammatically the early stages of the Riccia embryogeny as determined by Hofmeister and Kienitz-Gerloff. The first wall is approximately transverse to the axis of the archegone. Succeeding walls divide the embryo into nearly equal

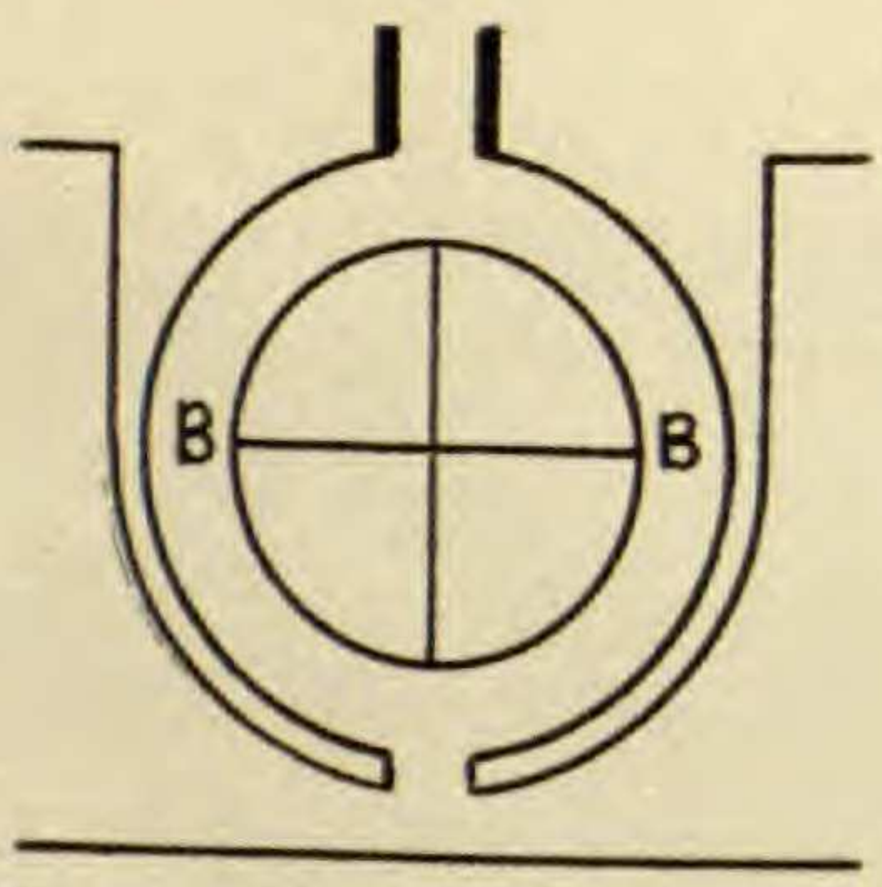

FIG. 1.—Embryo of Riccia.

[1] Vergleich. Unters. 47. 1851.

[2] Vergleich. Unters. über die Entwickelungsgesch. des Lebermoos-Sporogonium. Bot. Zeit. 32:166. 1874.

[3] Unters. über Lebermoos. 4:22. 1879.

octants. Alone among Bryophyta the embryo of Riccia (including here also the closely allied genera Ricciocarpus and Ricciella) shows very slight distal-proximal specialization, if any. The archegone stands perpendicularly upon the thallus, invaginated for protection, and the originally distal hemisphere develops in essentially the same manner as the proximal. The mature sporophyte, a globular body less than a millimeter in diameter, consists merely of a one-layered wall of sterile cells surrounding a homogeneous mass of spores, elaters being absent. The spores are released by disruption of the wall and disorganization of the surrounding tissues of the invaginated thallus and the calyptra.

Embryogeny of Sphærocarpus.— This interesting little plant was not carefully investigated until 1867, when Petounnikow made out some of the principal points in the embryogeny[4] after the early stages which apparently he did not see. In 1875 Kienitz-Gerloff[5] took in hand the investigation of this plant and practically completed it. He showed that while a considerable irregularity existed in young stages, the first wall was approximately transverse. This was succeeded by one or two other transverse walls principally in the hypobasal hemisphere, and finally periclines and anticlines in the epibasal hemisphere served to delimit the amphithecium and endothecium of the capsule. Leitgeb[6] gives a series of figures of the young embryo which together with the excellent series of Kienitz-Gerloff in the paper cited may be regarded as complete. Leitgeb suggests that its embryogeny "strongly resembles that of Fossombronia," but its resemblance seems strongest with the Marchantiaceæ, and probably the place of the plant is not with the Jungermanniaceæ as some taxonomists have thought, but with the simpler relatives of Marchantia. The mature sporophyte is a spherical capsule provided

[4] Sur les organes reproducteurs du *Sphærocarpus terrestris* Mich. Bull. Soc. Bot. de France 14:137. 1867.

[5] Neue Beitr. zur Entwickelungsgesch. des Lebermoos-Sporogoniums. Bot. Zeit. 33:795. 1875.

[6] Op. cit. 4:69. *pl. 9.* 1879.

with a short foot with bulbous base. Elaters are not present but nutritive cells are found among the functional spore mother cells. In *fig. 2* a diagram of the egg orientation and first segmentation is shown. The black epibasal segment is the ultimately sporogenous area, while the white hypobasal segment does not produce spore mother cells but is sterilized. The distal-proximal specialization which arises in the sporophyte is thus seen to be connected with the first segmentation plane of the egg. As will be noted in the next plant but one examined, such distal-proximal specialization need not necessarily be foreshadowed by the first segmentation plane.

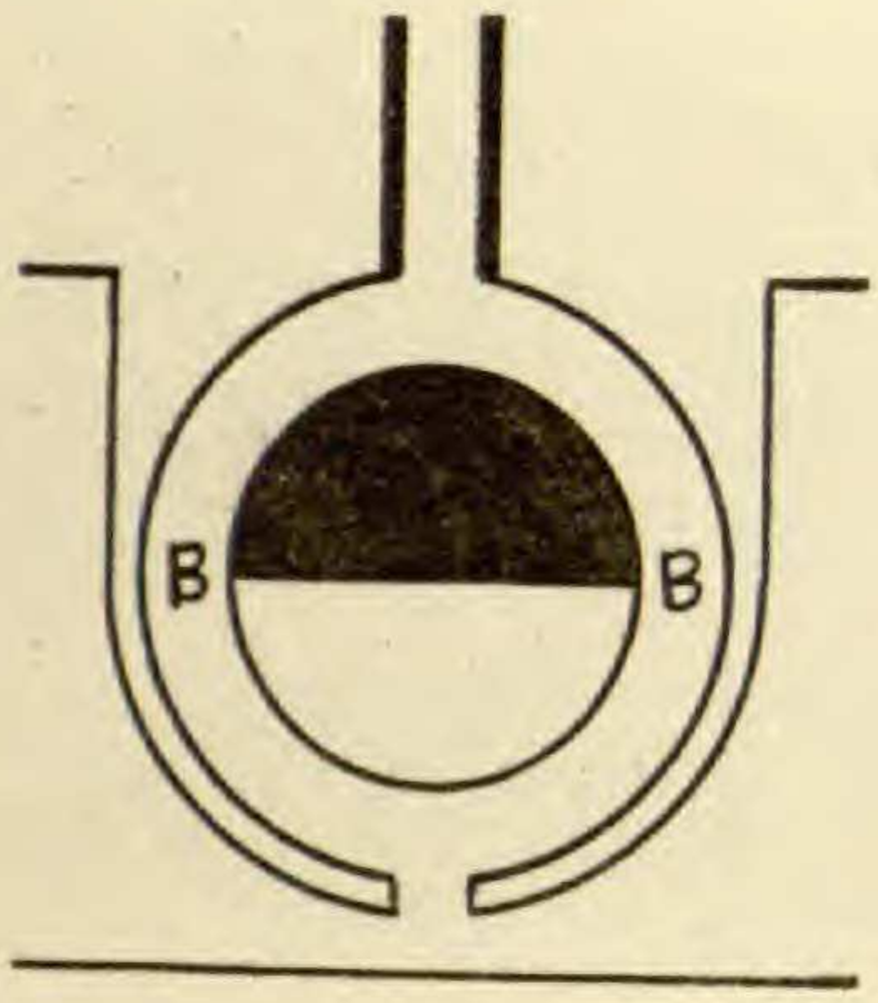

FIG. 2.—Embryo of Sphærocarpus.

Embryogeny of Marchantia.—This genus was studied by Hofmeister,[7] who investigated the embryo of *Marchantia polymorpha*. In the work cited his *pl. 11, fig. 16* shows an octant stage; *fig. 30*, of the related plant *Conocephalus conicus*, shows less correctly an early stage in the embryogeny provided with an apical cell which does not then exist. As in the case of the plants previously mentioned, the important researches on the embryo of Marchantia were made by Kienitz-Gerloff[8] whose *pl. 3* in the memoir cited gives eleven figures of young embryos from the quadrant stage up to the differentiation of foot and capsule and the development of wall and archesporium. In all essential particulars this embryogeny resembles that of Sphærocarpus except that secondary transverse walls parallel to the basal wall are not formed in advance of anticlines and periclines in the capsular region. The mature sporophyte is an ovoid or spherical capsule upon a short cylindrical foot which elongates during the last stages of maturation and projects the capsule beyond

[7] Op. cit. 56. 1851.

[8] Vergleich. Unters. u. s. w. Bot. Zeit. 32: 167. 1874.

the calyptra. In one particular, however, there is pretty generally in the Marchantiaceæ of higher rank than Sphærocarpus a modification of the primitive position of the sporophyte with reference to the horizon. Instead of being erect it is inverted more or less completely. This is due to the inversion of the archegone which, although developed dorsally on the thallus, is carried into a ventral position by displacements of growth, so that the neck of the archegone points towards the substratum. As the archegone is carried to an inverted position the egg must also be unless it rotates in the venter, a process which does not take place in ontogeny although apparently it does in phylogeny. *Fig. 3* shows in diagrammatic fashion the first segmentation stage of the Marchantia egg with the epibasal hemisphere shown black as before and now directed downward instead of upward. In either case, however, whether the embryo of Sphærocarpus or Marchantia be considered, it must be noted that the epibasal hemisphere is essentially the distal segment of the egg, while the hypobasal is as essentially the proximal. In Bryophyta a strong distinction arises between these differently situated segments and in pteridophytic types of embryogeny where the egg is frequently rotated to one side or even inverted in the archegone under ecological stress, it is always possible to distinguish the segment which is the homologue of the originally distal segment and this, whatever its position in the archegone, or with the thallus or the horizon, is termed the epibasal segment. The conception of an epibasal and hypobasal segment is therefore seen to be one of phylogeny rather than of embryogeny.

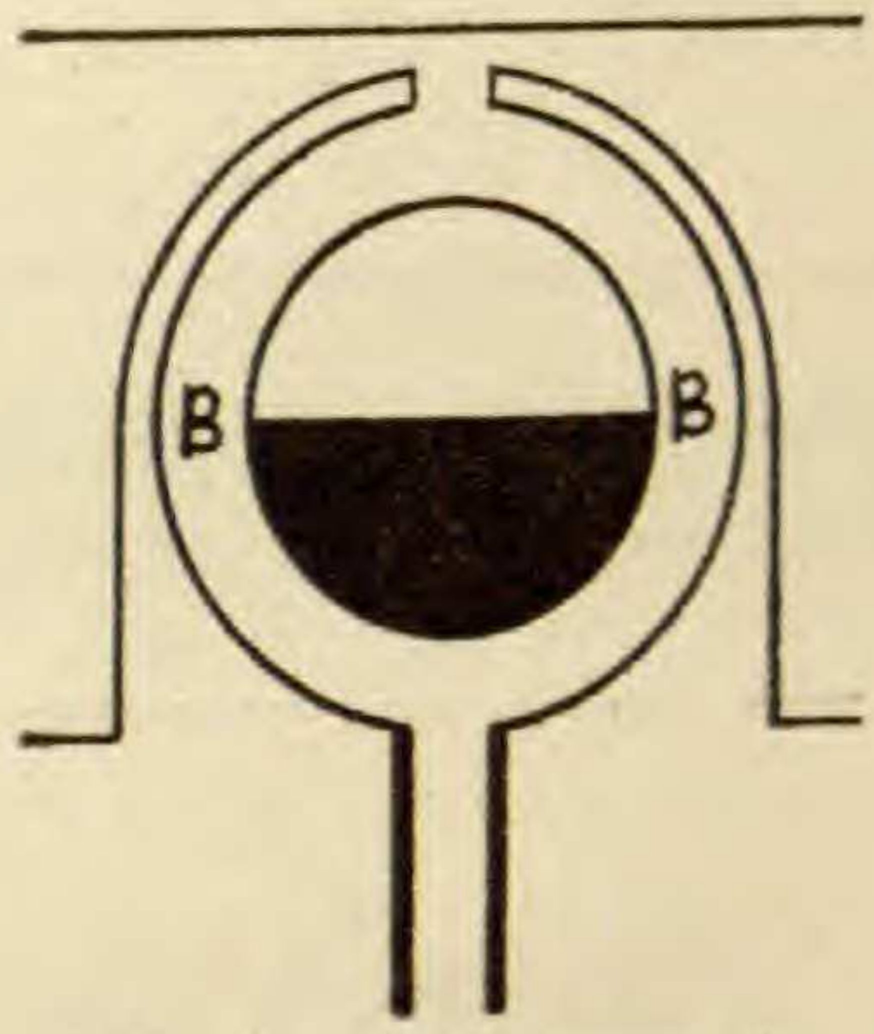

FIG. 3.—Embryo of Marchantia.

Embryogeny of Anthoceros.—While important work on the sporophyte of Anthoceros was accomplished by Schacht[9] in

[9] Beitr. zur Entwickelungsgesch. der Frucht und Spore von *Anthoceros laevis*. Bot. Zeit. 8:457. 1850.

1849, it was not until Hofmeister showed the independence of the rudimentary spore-producing organism from the thallus that a clear idea was possible of the early stages. Schacht's *pl. 6, fig. 2*, of the work cited, shows a young sporophyte of about twenty cells, but drawn as if a branch of the thallus. The position of the walls, however, is correctly indicated. Hofmeister,[10] in 1851, cleared up the embryogeny of this plant so far as concerned the first segmentations. His *pl. 1, fig. 36* of the work cited is practically correct, although not so much can be said for *fig. 39*. It is to Leitgeb and Waldner that we owe the modern knowledge of the Anthoceros embryogeny. Leitgeb[11] first discussed it fully in a special paper, and later Leitgeb and Waldner,[12] in their joint part of Leitgeb's classic work on the Hepaticæ, described and figured with accuracy the young plants from the first segmentation on to maturity. In Leitgeb and Waldner's memoir, *pl. 1, fig. 1* shows most clearly a young eight-celled stage, while earlier phases are described in the text. The originally formed wall is in this plant not the basal wall, but the median or transverse wall, running parallel with the axis of the archegone and dividing the egg into two halves, either anterior-posterior or right and left, since the archegone occupies a perpendicular position imbedded in the upper layers of the thallus. *Fig. 4* shows the ovoid shape of the egg, the vertical plane of the first segmentation, and the later formed plane of the basal wall which divides the egg into capsular area and foot area quite as in the Marchantiaceæ. In this egg the distal-proximal specialization is strongly marked. Not only does this appear in the position of the basal wall below the middle of the egg, but in the ovoid shape of the egg itself. The slender, columnar form

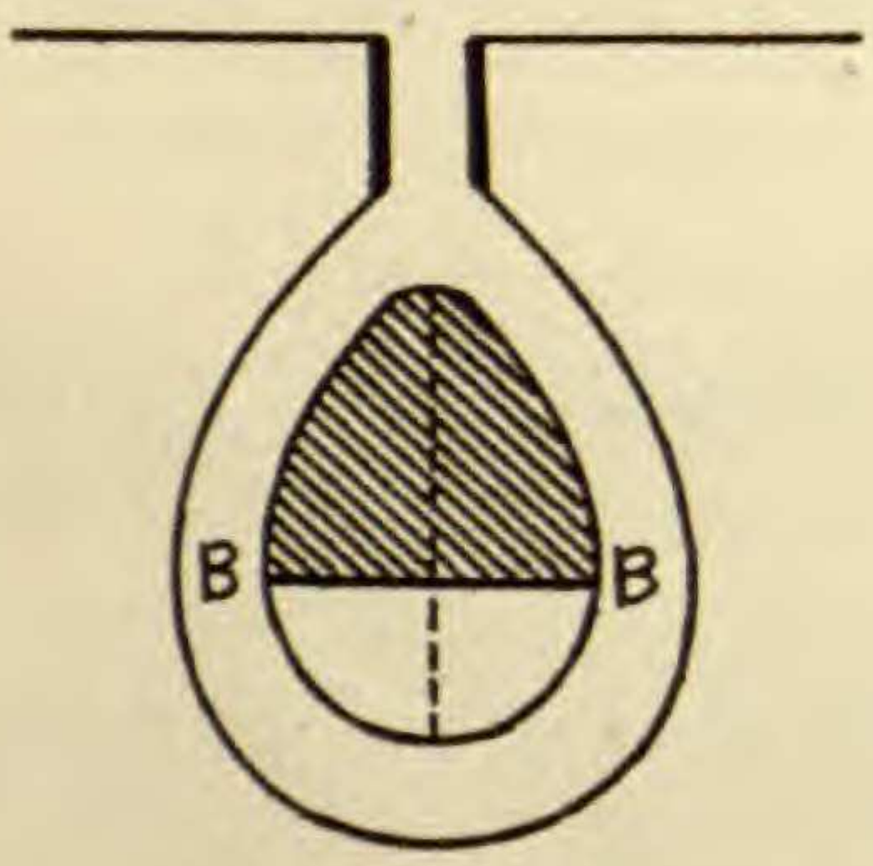

FIG. 4.—Embryo of Anthoceros.

[10] Op. cit. 5. 1851.

[11] Entwickelung der Kapsel von Anthoceros. Sitz. der K. Acad. Wiss. 73.

[12] Unters. über der Lebermoose 5: 21.

of the Anthoceros capsule capable of evolutional modification into the capsule of Sphagnum on the one hand, or the strobilus of Phylloglossum on the other, is prefigured to a degree in the egg. That the basal wall should not be the first wall formed is apparently a peculiarity not confined to this genus of plants, for in fern embryogeny the same irregularity has been noted. From the further development of the segments it is quite clear that the vertical wall first formed is by no means basal, as it is in Pilularia, and the only explanation at all satisfactory is the one given here, that it is in reality median or transverse.

Embryogeny of the Jungermanniaceæ.—In this important family of Hepaticæ there is no new type developed. Strong distal-proximal specialization is universal, and the base of the capsular tract is converted into a sterilized stalk, so that the elevation of the sporogenous area is brought about by an organ derived from the epibasal hemisphere, rather than from the hypobasal, as in Sphærocarpus. In Marchantiaceæ, as is well known, the elevation of the sporogenous area is a function not of any sporophytic organ, but principally of the archegoniophore stalk which elongates, carrying up into the air the circle of attached sporogonia. In Fossombronia, Pellia, Frullania, Lejeunia, and the other Jungermanniaceæ the embryogeny is of essentially the type described for Sphærocarpus. An additional elongation of the sporophyte is provided for in the manner described, but in general the diagram of the Sphærocarpus embryo would suffice for that of any of the others, as for any moss.

Comparison of bryophytic types of orientation and segmentation.—A glance at the figures will show that there is really but one type of egg orientation represented in this group. In Riccia there is no sharp differentiation between the epibasal and hypobasal hemispheres so far as concerns their further development. In the higher genera the hypobasal segment is invariably sterilized, while the epibasal hemisphere is wholly or in part developed into a capsular body, maturing spores with or without accessory cells in the form of nutritive cells, elaters, or columella cells. In all cases the hypobasal hemisphere is proximal, while the epibasal is distal. The archegone may be erect, horizontal or inverted, but the orientation is always normal and primitive; that is to say, the epibasal hemisphere, originating as the distal half of the egg, retains constantly the distal position. This distal-proximal arrangement of the first egg segments is not disturbed in any important sense by the retardation of the basal plane in such an embryo as that of Anthoceros. Without further discussion at this point, it may be well to pass at once to the consideration of pteridophytic embryogenies, in order that their new developments may be brought before the attention.

PTERIDOPHYTIC ORIENTATION AND SEGMENTATION TYPES

Among certain genera of pteridophytes it is probable that the primitive bryophytic orientation of the egg is retained. Among others it is profoundly altered, so that the inverted embryogeny of the Lycopodinæ and of the leptosporangiate ferns presents itself for consideration. It will be shown later that the inverted embryo of the club-mosses and the semi-inverted embryos of Polypodium and Alsophila are not directly comparable, the inversion having originated under probably different stimuli in the ancestral types; that is, in a word, there is not one type of inverted orientation to be set over against the one primitive type of normal orientation. On the contrary, inversion, semi-inversion, or rotation of the egg may be shown to have arisen in different phyla under different conditions.

Embryogeny of Equisetum.—This plant was among those studied by Hofmeister,[13] who gives some correct figures of early stages in *pl. 17* of the work cited. His *fig. 16* is particularly excellent. The very early two-celled stage of the embryo is not shown, but the horizontal first division plane is duly announced.

[13] Ueber die Keimung der Equisetaceen. Abh. K. S. Gesellsch. d. Wiss. 4: 174.

Sadebeck[14] gave a full account of the Equisetum embryogeny in 1878, and his figures serve to illuminate all the important stages. The basal wall divides the egg into a distal half as distinguished from a proximal. The distal or epibasal hemisphere develops into the shoot tract, while the proximal retains its ancestral character of a foot from which, however, the root springs endogenously (*fig. 5*). It may be regarded, I think, that the type of embryogeny shown by Equisetum is the most primitive among pteridophytes, and indicates the probable phylogenetic significance of the root as an embryonic organ of Pteridophyta. The root is developed as an emergence from the conduction-path of the nursing foot. Throughout the vegetable kingdom it almost universally arises from internal tissues, and may be regarded as a branch of the stele. The precise behavior of the hypobasal hemisphere of Equisetum, which enlarges by cell-division and growth into a bulbous body and then develops a root from an apical cell, not superficial, may be taken for a recapitulation of the original evolution of the root as an organ of the sporophyte. In this sense root is not homologous with stem, and is, indeed, a new structure. It seems to be, for the archegoniate series of plants, essentially first of all an absorptive tract, and it comes into existence through adaptation to its surroundings of the sporophyte endowed with a progressively larger photosynthetic area. This conception is in direct contradistinction to an older view, that root as a morphological area is merely the proximal end of the axis, and that its primitive function was support rather than absorption.

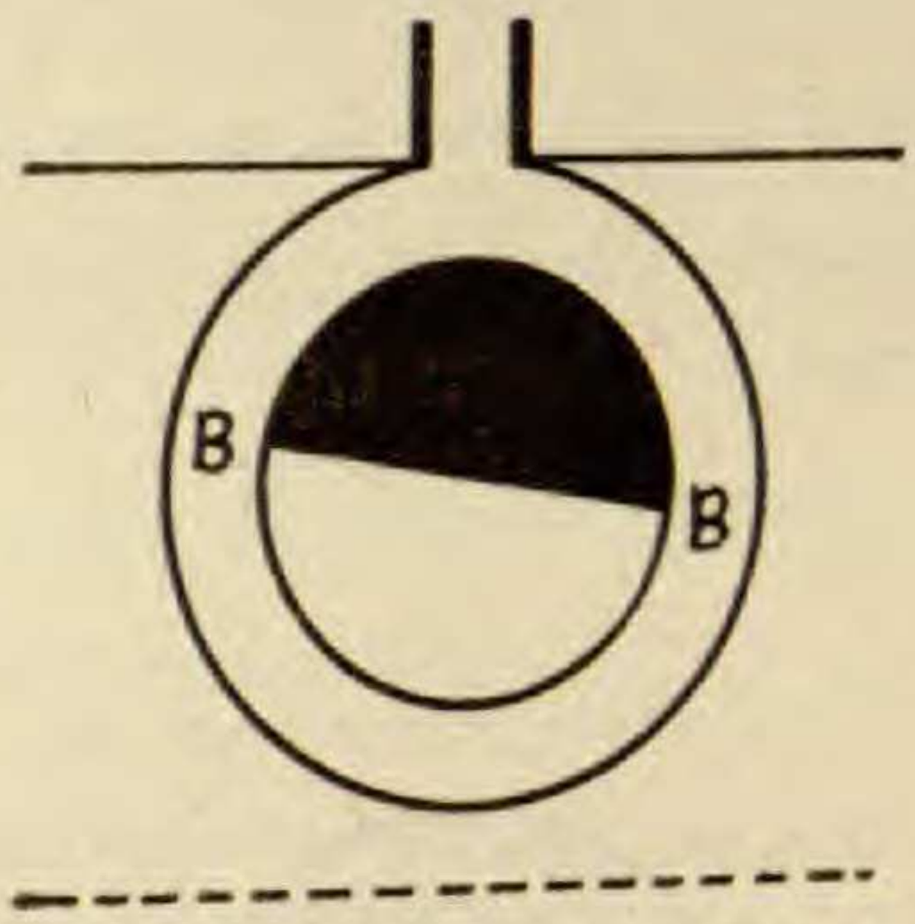

FIG. 5.—Embryo of Equisetum.

Embryogeny of Angiopteris.—Our knowledge of the early stages in the development of the Angiopteris sporophyte is due

[14] Die Entwickelung des Keimes der Schachtelhalme. Jahrb. Wiss. Bot. 11:575. 1878.

to Farmer[15] who has carefully investigated the first segmentations. The archegones are situated upon the lower side of the rather thick and massive prothallium. The eggs segment by a transverse basal wall followed by a median. Unlike the egg of Marchantia this egg of Angiopteris retains its original orientation with reference to the horizon, although the archegone is displaced, for protection, to the lower surface of the prothallium. The epibasal hemisphere is directed upward, hence away from the neck of the archegone, and the egg must be conceived to have rotated in the reverse direction to the archegone as it passed from the original dorsal position, as in Anthoceros, to the ventral position generally characteristic of the ferns. *Fig. 6* shows the position of the egg and its segments in the inverted archegone, and should be compared with *fig. 3*, that of Marchantia, where the inversion takes place during ontogeny and the egg is not rotated. In Angiopteris and the other Marattiaceæ which have been studied, this inversion does not take place as in Marchantia, during the life of an individual prothallium, but has evidently resulted from a slow adaptation. Opportunity has thus been given for the egg to change its position from time to time as the slight inclination of the archegone made necessary, if it was to retain its normal position with reference to the surface of the substratum. Consequently the Angiopteris stem and cotyledon bore through the prothallium, and thus come to independent illumination and the plant develops its sporangia a sufficient distance above the substratum to insure spore distribution.

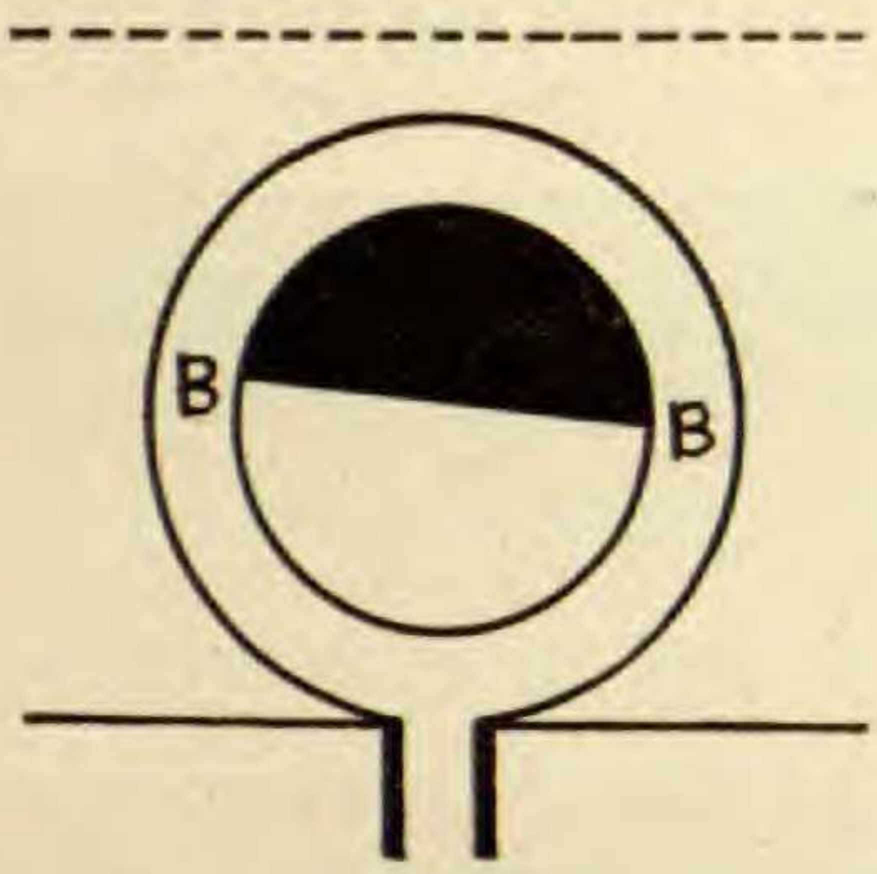

FIG. 6.—Embryo of Angiopteris.

Embryogeny of Isoetes.—The embryogeny of this plant has been studied by a number of observers of different degrees of ability, but, it seems to the writer, has never received the proper

[15] On the embryogeny of *Angiopteris evecta*. Ann. of Bot. 6: 265. 1892.

interpretation. Hofmeister's[16] classic memoir is the first paper of importance that deals with the embryogeny. In *pl. 2, fig. 20* of the work cited he figures the first segmentation stage, and in *fig. 21* shows an octant stage. Other less correct intermediate stages are figured in *pl. 3*, but the *fig. 13*, which gives a view of an embryo with developed cotyledon, is excellent. Nearly thirty years later Kienitz-Gerloff[17] undertook an examination of this plant, and concluded a research characterized by accurate observation of the earlier stages, coupled with erroneous conception of the later. His series of figures in the work cited carry the embryo from the stage just succeeding the octant stage up to ligular development. Farmer[18] in 1890 incidentally considered the embryogeny and came to the conclusion that the first root was adventitious.

The segmentation of the Isoetes egg is briefly as follows: The egg is cleft by a wall nearly perpendicular to the axis of archegone. From the hemisphere next the archegone neck, after quadrant and octant walls have appeared, are developed the cotyledon, the root, and, later, probably from the cotyledon quadrant (not the root quadrant as has been suggested), the stem. The hemisphere away from the neck develops only a mass of cells, which has been generally considered as the foot, and so described. Now the development of a primary root from the epibasal hemisphere is so difficult an hypothesis to accept that Farmer's solution of the dilemma by considering the first root an adventitious organ would necessarily be adopted if another explanation were not at hand. It can properly be questioned, however, whether the first transverse wall formed is really the basal wall. This has been the current hypothesis, and Isoetes in its embryogeny has been compared with Equisetum, a plant which manifests, as has been indicated above, the normal bryophyte type of orientation of its egg. If, how-

[16] Zur Entwickelungsgeschichte der *Isoetes lacustris*. Abh. K. S. Gesellsch. Wiss. 4: 131.

[17] Ueber Wachsthum und Zelltheilung und die Entwickelung des Embryos von *Isoetes lacustris*. Bot. Zeit. 39: 761. 1881.

[18] On *Isoetes lacustris*. Ann. of Bot. 5: 37. 1890.

ever, it be supposed that, as is certainly the case in Anthoceros, the first wall formed in the Isoetes embryo is not the basal wall, but the transverse, there is much less difficulty. It is then possible to see how the root and foot may develop from the hypobasal hemisphere, not shaded in *fig.* 7, while from the epibasal develops the strong cotyledon and a group of irregular cells which are generally regarded as constituting a portion of the foot, but should more probably be considered to be a poorly developed leaf-structure. Only half of what has been considered foot in the Isoetes embryo is here retained in that morphological category. The remainder is considered to be aborted leaf functioning as foot. The true epibasal area gives rise to the shoot while the true hypobasal area gives rise to the root. Thus the difficulty of supposing root to originate from an epibasal hemisphere is readily avoided, and by analogy with Anthoceros no violence is done to accepted ideas of embryology. In brief an Isoetes egg may be regarded as an Angiopteris egg turned through an angle of 90° in the archegone cavity, and cut by the transverse wall before the epibasal wall appears.

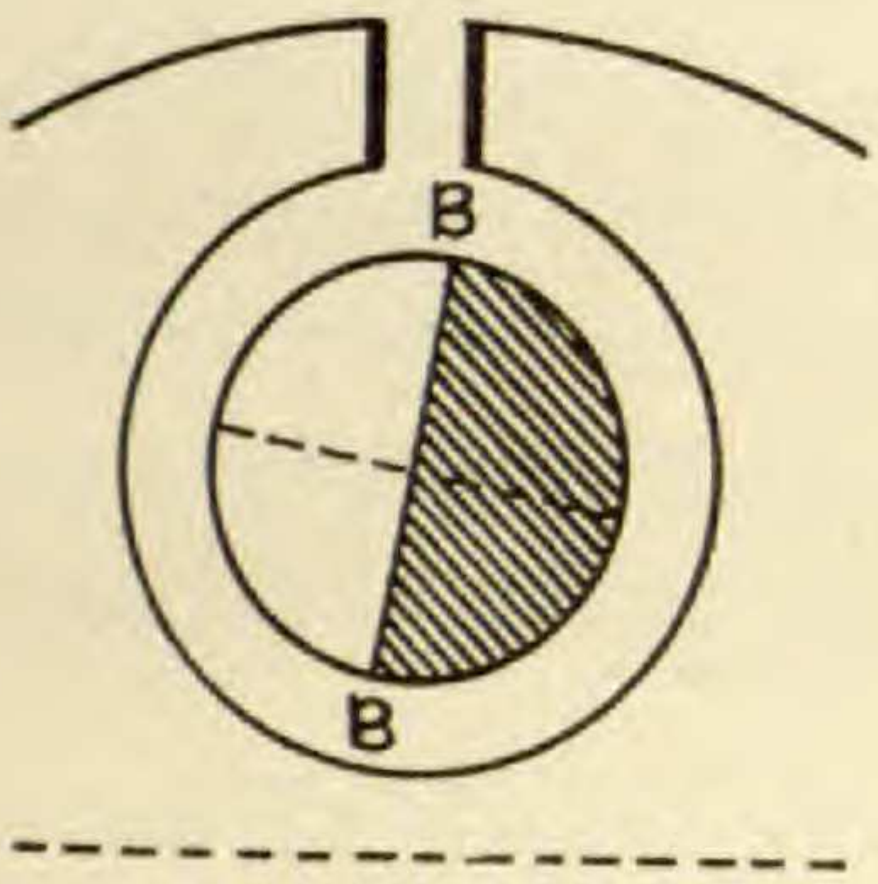

FIG. 7.—Embyro of Isoetes.

Embryogeny of Pteris.—The leptosporangiate fern embryo has been studied by a large number of observers, the first thorough work being that of Hofmeister,[20] who made out correctly the first divisions. As in the case of many of the lower plants the complete study was accomplished later by other observers. Goebel[21] contributed some important observations in a paper primarily devoted to prothallial structure, and Kienitz-Gerloff[22]

[20] Ueber Entwickelungsgeschichte und Bau der Vegetationsorgane der Farnkräuter. Abh. K. S. Gesellsch. Wiss. 5: 615.

[21] Entwickelungsgeschichte des Prothalliums von *Gymnogramme leptophylla*. Bot. Zeit. 35: 689. 1877.

[22] Untersuchungen über die Entwickelungsgeschichte der Laubmoos-Kapsel und die Embryo-Entwickelung einigen Polypodiaceen. Bot. Zeit. 36: 49. 1878.

investigated the embryos of Pteris, Aspidium, Adiantum, and Gymnogramme, giving in his *pl. 3* the figures of Pteris embryogeny which have become classic. The first wall in the Pteris embryo runs almost parallel with the archegonial axis, transverse to the prothallium, and divides the egg into a smaller anterior epibasal and a larger posterior hypobasal hemisphere. The normal position of the archegone is ventral, so that at first the root and foot octants are directed obliquely ward. If, however, the archegone is abnormally produced upon the upper side or (sometimes normally) upon the margin of the prothallium the orientation is not essentially modified with reference to the archegone. This is the reverse of the condition observed in Marchantia, but, as in the liverwort, there is no revolving of the egg in its archegone venter. *Fig. 8* shows the normal position of the egg, the epibasal hemisphere being directed toward the morphological apex of the prothallium and obliquely toward the substratum.

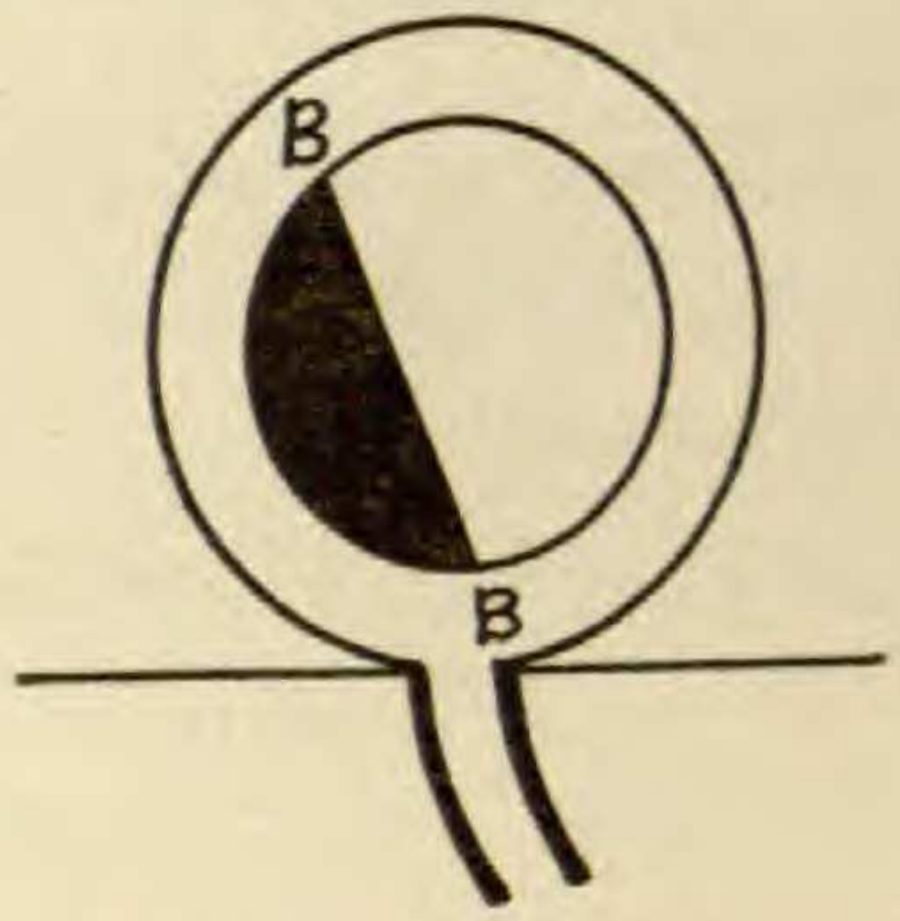

FIG. 8. Embryo of Pteris.

Embryogeny of Marsilia.—The Hydropterideæ have received their share of investigation during the last fifty years. Hofmeister[23] in 1851 examined the embryo of Pilularia, and later Hanstein[24] made a very complete study of the Marsilia embryogeny, offering in *pl. 11* of the work cited numerous satisfactory figures of the early stages. As in other leptosporangiate and, indeed, as in all heterosporous ferns, the basal wall is parallel with the axis of the archegone. Here, however, unlike Isoetes, the

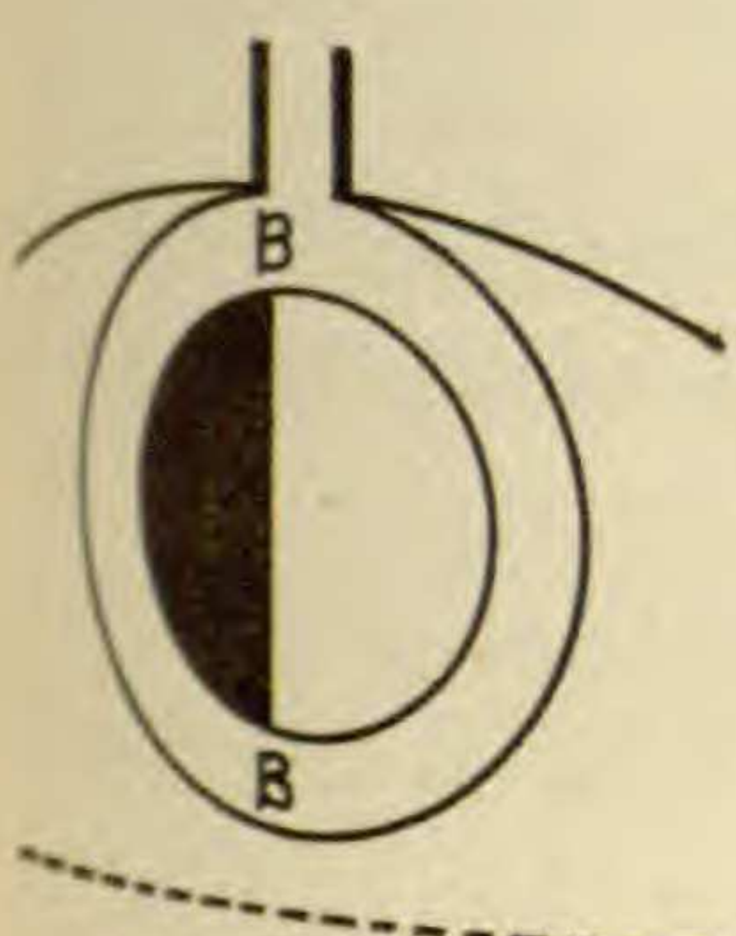

FIG. 9.—Embryo of Marsilia.

23 Vergleich. Unters. 106. 1851.

24 Die Befruchtung und Entwickelung der Gattung Marsilia. Jahrb. wiss. Bot. 4: 197. 1866.

first wall to form is the basal wall, separating, as in Pteris, a smaller laterally-placed epibasal hemisphere from a larger hypobasal. In *fig. 9* the orientation is indicated as described, and the further development of the hemispheres, as in the case of Pteris, is too well known to need any extended description.

Embryogeny of Lycopodium.— For many years the sole investigated lycopodineous embryo was that of Selaginella so ably studied by Pfeffer,[25] but in 1884 Treub[26] presented the first figure of an embryonic Lycopodium plant, something which had been diligently looked for during many previous years. In this first paper the account was incomplete, but two years later Treub[27] was able to announce most of the stages in the embryogeny of *Lycopodium phlegmaria.* Confirmation of Treub's researches was given within a year by Goebel,[28] who, however, does not figure any young stages of the embryos studied by him, his sketch of the young plant of *Lycopodium inundatum* being about as far along in development as was Treub's *Lycopodium cernuum* embryo of his 1884 contribution. From the brilliant investigations of Treub and Pfeffer in particular the embryogeny of the Lycopodinæ may now be said to be thoroughly known, although as for so many other groups the foundation here was really laid by Hofmeister,[29] who figured as long ago as 1851 a two-celled embryo of *Selaginella denticulata,* and showed the peculiar suspensor in its proper relation to the rest of the embryo. In Lycopodium, more instructive than Selaginella because its prothallium is less vestigial, the archegones may be regarded as dorsal, and the egg within the archegone segments perpendicularly to the archegone axis, as in Equisetum. It is, however, the hemisphere towards the base of the archegone

[25] Die Entwickelungs. des Keimes der Gattung Selaginella. Hanst. Bot. Abh. 1:32. 1871.

[26] Études sur les Lycopodiacees. Ann. Jard. Buitenzorg 4:129. 1884.

[27] Études sur les Lycopodiacees. Ann. Jard. Buitenzorg 5:115. 1886.

[28] Ueber Prothallium und Keimpflanzen von *Lycopodium inundatum.* Bot. Zeit. 45:169. 1887.

[29] Vergleich. Unters.

which has the power of principal development, and it is therefore this hemisphere which must be regarded as epibasal. The hemisphere toward the archegone neck forms the well-known suspensor-cell, and is clearly the homologue of the foot in mosses, liverworts, equisetums, and ferns. The first root in Lycopodium and Selaginella together with a nursing organ, misnamed the "foot," arise adventitiously from the epibasal hemisphere. As compared, then, with Equisetum the egg of Lycopodium must be regarded as having undergone rotation through an angle of 180°, bringing the primitive hemispheres into a position just the reverse of their original one.

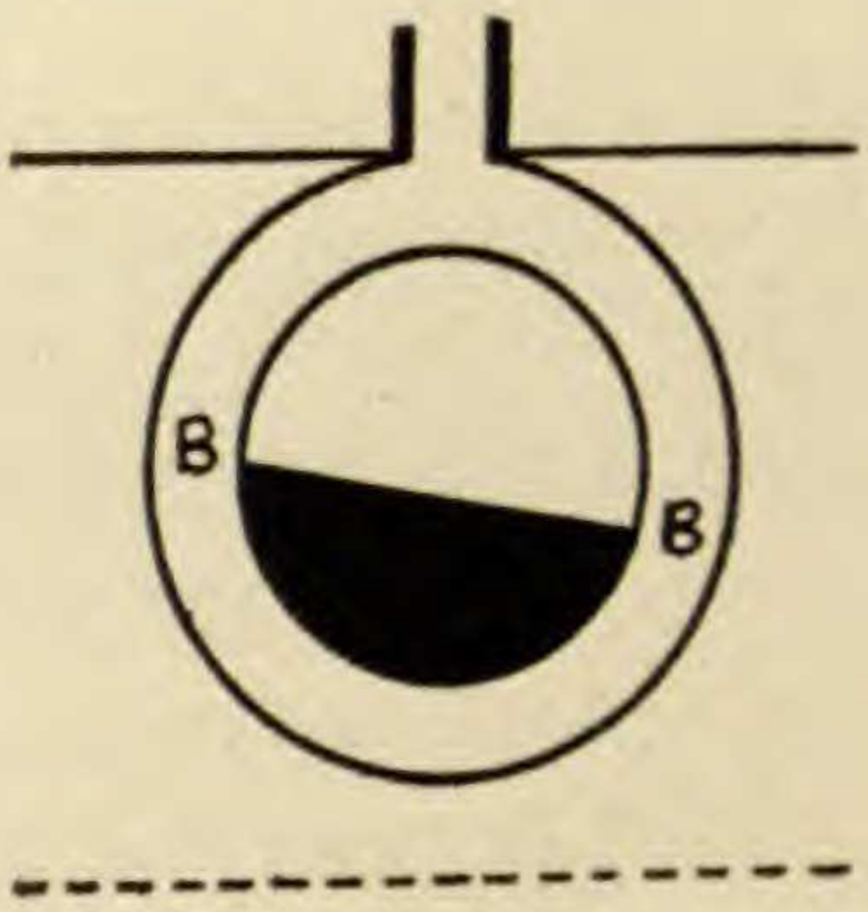

FIG. 10.—Embryo of Lycopodium.

Comparison of pteridophytic types of orientation and segmentation.—It seems to assist toward a clear conception of pteridophytic embryogeny to regard Equisetum as manifesting the primitive orientation and segmentation, and to interpret the other types as derivations, primary or secondary, from this fundamental bryophyte-like method. The Pteris and Lycopodium embryogenies may be considered as modifications due to adaptation. There are then at least these principal types:

A. Primitive orientation, *e.g.*, Equisetum.

B. Semi-inverted orientation, *e.g.*, Pteris.

C. Inverted orientation, *e.g.*, Lycopodium.

It will be noted that the type of Angiopteris must be connected with that of Equisetum. The hemispheres of the Angiopteris embryo lie in the original plane with reference to the substratum, the epibasal distally and the hypobasal proximally. Owing to the modified position of the archegone, on the ventral rather than on the dorsal side of the thallus, the epibasal hemisphere while retaining its primitive position with reference to the substratum comes into an entirely reversed position with reference to the archegone. The epibasal hemisphere now faces the base of the archegone instead of the neck. If it be accepted that the new position of the Angiopteris archegone as compared with the position of the same organ in the archetypal Anthoceros is an adaptation for protection it is apparent that class A above is easily divided into two subclasses as follows:

A. Primitive orientation.

1. Archegone in original position, *e. g.*, Equisetum.
2. Archegone in adaptive position, *e. g.*, Angiopteris.

To interpret the semi-inverted orientation of Pteris from the conditions in Angiopteris is possible if we regard it as a further adaptive modification. It may be conceived to be of advantage to the young embryo to grow through the least resistant tissues of the prothallium upon the ventral side of which it had originated. Any tipping of the egg so that the epibasal hemisphere should incline towards the growing point of the prothallium would subserve this end, and at the same time would more definitely place the absorptive hypobasal area in the most advantageous position with reference to the older, nutriment-containing portion of the gametophyte. Such an adaptive tipping forward of the epibasal hemisphere would be perpetuated, and at the same time might be accentuated until the change in position exceeded 90° as is the case if one compares Pteris with Angiopteris. The position, then, of the epibasal hemisphere of the Pteris embryo has an interesting suggestion concerning the phylogenetic history of the prothallium. Clearly the delicate almost unilamellar prothallium of the Polypodiaceæ offers slight resistance even if an embryo were to penetrate it directly with its cotyledon or stem-apex. Therefore it seems reasonable to regard the semi-inverted embryo as suggesting that the ancestral prothallia were much thicker, and that the habit of tipping forward dates from the time of thick prothallia. This is precisely in accord with many other bits of evidence all of which bear toward the same conclusion. And, *pari passu*, the position of the embryo in Trichomanes, suggesting as it does the reduced character of the filamentous prothallium, renders it difficult to connect the Hymenophyllaceæ directly with the bryophytes, as was the custom of the older pteridologists.

There is naturally no difficulty presented by the embryogeny of Marsilia, nor by that of the closely related Pilularia or of the not distant Salviniaceæ. In all of the Hydropterideæ the semi-inverted leptosporangiate fern embryogeny persists, except that the angle of variation from the original position is here quite exactly 90°. This perpendicular position of the basal wall may be in some way an adaptation to heterosporous conditions, and may be connected with the positions of the nursing foot and of the emergent cotyledon and stem-apex. At any rate, it characterizes Isoetes, as explained above, and may be said to be the mark of all heterosporous pteridophytes of which the embryo is not provided with a suspensor. Two subclasses, therefore, may be defined under class B above:

B. Semi-inverted orientation.
  1. Sequence of segmentation planes normal, *e. g.*, Pteris.
  2. Sequence of segmentation planes abnormal, *e. g.*, Isoetes.

In the case of a plant so strongly isolated as is Iscetes speculation is scarcely profitable in an attempt to explain the origin of the perpendicular basal wall. It may have been derived from either an Equisetum-like or Angiopteris-like, or even Pteris-like ancestral form. Certainly it is of all pteridophytic types the most disconnected, as it is in some respects the most peculiar. Whether the original tip-to-one-side began to characterize its embryo because a resistant prothallial mass lay between the embryo and the outer world, or because homosporous conditions were gradually changed to heterosporous, and the nutriment supply and the megaspore wall exerted an influence upon the position of the young hemispheres, in any case the position must be regarded as one of adaptation. Just how the adaptive position arose in this plant will possibly never be certainly suggested.

The inverted egg of the Lycopodinæ is very easily explained, so far as the nature of the adaptation is concerned. Plainly enough the use of the suspensor or foot-homologue is to push the epibasal hemisphere into the center of the prothallium where the food-supply will most abundantly and symmetrically surround the developing segment. But to explain in any reasonable way how this remarkable inversion of the egg originated is quite another matter. The archegone in Lycopodium may be regarded as occupying a dorsal position on the thallus as in the case of Anthoceros. The Lycopodium prothallium, as seen in a primitive type like that of *Lycopodium cernuum*, not modified by adaptation to saprophytic nutrition, is comparable with an Anthoceros thallus, not only in the origin of the sexual organs but in the vegetative tract also. Yet it is inconceivable, I think, how an egg developing after the manner of an Anthoceros egg should invert itself in the archegone, convert its foot into a suspensor, and develop from its abnormally oriented epibasal cell the stem-axis and an adventitious nursing and absorptive tract. The inverted position of the Lycopodium egg cannot then be regarded as a primitive modification of the Anthoceros conditions. Rather would it appear that between the Anthoceros embryogeny and the Lycopodium embryogeny some other type had intervened.

It is possible, though no doubt extremely speculative, to refer the inversion of the Lycopodium egg to a double displacement, under adaptive conditions, of the archegone in the ancestral forms. While the archegone was situated on the ventral side of the prothallium the tipping of the embryo took place as in the ancestors of the Polypodiaceæ; following this the archegone worked back to the upper surface of the prothallium carrying the egg in its derived position. As the archegone returned, in successive generations, more and more to the ancient dorsal position, the embryo adapted itself to the most favorable position for nutrition and subsequent development, and when heterospory originated, the Selaginella type, in which the embryonic epibasal tract is immediately thrust into the center of the spore by the elongation of the primitive foot area, came into existence. Such an epibasal area of the embryo so placed must have early begun the development of an adventitious "foot" and root.

PHANEROGAMIC ORIENTATION AND SEGMENTATION TYPES.

All segmentation types among flowering plants, with the possible exception of that manifested by the extraordinary plant *Ginkgo biloba*, are referable to class C. Various secondary ecologic modifications have arisen, the most remarkable being the meroblastic segmentation in Coniferæ, the free-nuclear segmentation in the Gnetales—a phenomenon ecologically comparable to the free-nuclear origin of female prothallial tissues in Selaginella or to endosperm origin in most seed-plants—and the reduction of the suspensor, as in Pistia, Listera, Cypripedium, the Mimoseæ and Hedysareæ among others. It is not possible, however, to name any suspensorless flowering plant embryo except that of *Ginkgo biloba*, in which the absence of suspensor is not plainly and unmistakably a secondary adaptation. In Ginkgo alone is there a suggestion that the embryogeny belongs to the general fern type rather than to the lycopodineous. Other well-known old and new facts about Ginkgo should be considered in this connection but will here be passed over without further notice.

GENERAL CONSIDERATIONS.

Adaptive phenomena in reproductive tracts.—Unquestionably, like all other organs of the plant, those concerned with reproduction are more or less exactly adapted to their environment. It is true they are less plastic than the organs of the vegetative tract, and hence do not show the epharmonic characters so variously as stem, root, and leaf structures may. For this reason they are quite universally, by modern as by ancient taxonomists, employed as the landmarks of phylogeny, not easily shifted by transitory outward influence. Yet form and structure not primarily connected with their special functions may be imprinted upon then and developed in them. Special positions are assigned them under outward stimulus, and their structure, shape, size, attitude, and behavior may all come to have some definite relation to the *melange* of forces and substances that surround them. Compare, by way of illustration, the almost globular form of the spermary in Anthoceros or Dendroceros, growing under a pressure exerted by the cellular roof of the schizogenetic cavity in which the organ develops, with the elongated cylindrical spermary of Polytrichum situated upon its short pedicel in the axil of a bract of its "inflorescence." The shape of the one differs from that of the other not on account of different reproductive specialization but purely because molded by lateral pressures while the other is subjected to vertical. Again a similar reaction to outward conditions is to be observed in the convexity anteriorly of the so-called "neck" of the Polypodium archegone. Evidently enough this curved cylinder, differing morphologically as well as ecologically from the straight true neck of a moss archegone, is a response in form to its acquired ventral position upon the prothallium and to the forward growth of the prostrate sexual plant. The convexity may be regarded as a purely adaptational phenomenon determined by a group of conditions among which are the growth habits of the prothallium, the ventral position of the archegone, the extension of the "neck," and the resistance and friction of the substratum.

The primitive position of the sexual organs seems more intimately reproductive in its significance, than adaptational. That is, the position upon the plant-body of the rudimentary egg-maturing or sperm-maturing cell is determined by the conditions of accurate reproductive functioning, and not until considerable organs are evolved do the purely adaptive changes become important. The well-known and closely related plants Œdogonium and Bulbochæte, from their simplicity are suggestive. In Œdogonium, which consists of unbranched filaments, the egg-cells are intercalated between vegetative cells. In Bulbochæte, however, where branching is common, distal-proximal specialization makes itself felt, and the oogonia and antheridia are disposed terminally upon the branches, bringing them to the general surface of the thallus where interference of closely packed branches will not hinder the egg-seeking, locomotive movements of the sperms. Together with this definite peripheral location of the sexual cells arises the need for protection of them from injurious impacts of all sorts and sharp bristling chætæ are developed. In many Hepaticæ by invagination, and in Musci by envelopment with bracts, the sexual organs are protected, and the exposure due to their morphologically peripheral position is modified or almost completely negatived. In Anthoceros the protective instinct results in the habit of developing the spermaries in actually closed cavities, not to be opened until the sperms are quite mature. Such derived positions while adaptational in the truest sense must be admitted to have important effects upon the reproductive rank of the organs or organisms in question.

Primitive reactions of segmenting eggs to their environment.—The first necessity that confronts a plant egg is that its position be such as to insure fecundation. That this may take place it is necessary that the egg should be protected against harmful influences, but should be exposed to the ingress of the sperm. After fecundation it is necessary that the embryo should be protected and nourished and that it should, with the least waste of matter or of energy, develop into a functional sporophyte. The function of a sporophyte may be briefly defined as the manufacture of as *many* and as *certainly germinable* spores as possible. Under such necessities the eggs are at first peripherally disposed with such protective layers about them as may have been developed and maintain this general position until spermatozoid-fecundation is abandoned, passing over through the Ginkgoales and Cycadales to pollen-tube fecundation.

The primitive segmentation-types as seen in Riccia may have originated under direct stimulus by the force of gravity, as has been suggested, but very early the direction of the basal wall became fixed with reference to the archegone axis and thereafter could be changed only in course of extended evolution. The distal-proximal specialization of the archetypal embryos, bringing into existence an epibasal as distinguished from a hypobasal hemisphere, was an immediate consequence of the two conditions already mentioned, viz., transverse segmentation and peripheral position of the archegones. The persistence of the function of sporogeny in the epibasal hemisphere cell-descendants, and the disappearance of this function from the hypobasal tract is a most natural division of labor, and in each area improvements for reproduction and for absorption have been steadily evolved. By the relations of the young embryo to the parent prothallium and by the ancestral relations, orientation is determined. This is an adaptive phenomenon.

Kienitz-Gerloff[30] in a general article suggests, without having considered, however, a very full series of forms, that torsions (Drehung) may explain the oblique position of the Pteris epibasal segment as compared with that of the mosses, seeming to propose a spontaneous shifting of the plane of segmentation. This explanation I am unable to accept for the whole group of positions seems to be clearly adaptive. In the paper cited, Kienitz-Gerloff gives four diagrammatic longitudinal optical sections of embryos illustrating his idea of lateral torsion. This paper is of interest also from its ingenious though faulty determinations of homologies between Bryophyta and Spermatophyta, in quite the manner of the older school of embryologists.

SUMMARY.

1. The orientation of the plant-egg is at bottom a phenomenon of adaptation.

2. The conception of a basal wall is founded upon facts of phylogeny so profound that it is necessary to recognize that wall as basal which separates morphologically distal from morphologically proximal regions. The first wall formed may or may not be the basal wall.

3. Three principal types of egg-orientation are recognized: the *primitive* or bryophytic, characteristic also of Equisetum and Angiopteris; the *semi-inverted*, characteristic of Isoetes and the

[30] Ueber den genetischen Zusammenhang der Moose mit den Gefässkryptogamen und Phanerogamen. Bot. Zeit. 34 : 705. 1876.

leptosporangiate ferns; and the *inverted*, characteristic of Lycopodinæ and Spermatophyta.

4. The origin of the primitive type is in adaptation to the peripheral position of the archegones and to the plane of the substratum; the origin of the semi-inverted type is in adaptation to derived archegonial positions and resistance of prothallial areas, interfering with the direct normal growth of the embryo; the origin of the inverted type is in adaptation to repeated archegonial displacements and nutritive qualities of prothallial areas adjacent.

5. The phylogenetic sequences derived from such an ecological investigation of embryos do not materially differ from those derived by a study of pure morphology.

University of Minnesota.